Experimental Researches on Vegetable Assimilation and Respiration.—XVI. *The Characteristics of Subnormal Photosynthetic Activity Resulting from Deficiency of Nutrient Salts.*

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When grown as a series of water-cultures, each deficient in one or other of the essential nutrient salts, plants of *Phaseolus vulgaris* all show a lowered photosynthetic activity. Comparison of the characteristics of this state with those of the lowered activity, due to old age, suggests that subnormal photosynthetic activity in general depends upon reduction of the effective chloroplast surface, and that the magnitude of this reacting surface must be a factor of fundamental importance in the quantitative determination of assimilation.

It is well known that deficiency of nutrient salts retards the general growth of plants, as measured by the increase of dry-weight. Since 90 per cent. of the dry-weight of plants is contributed by the process of photosynthesis, it follows that this retarded growth must result, directly or indirectly, from reduction in the amount of carbohydrate photosynthesized.

The average rate of assimilation of the whole plant may be decreased in two ways; by decreasing the average rate of assimilation per unit leaf-area, and by decreasing the total leaf-area of the plant. A reduction in the rate of assimilation per unit leaf-area would no doubt be reflected eventually in a smaller total leaf-area since there would be less material available for the building of new leaf tissue.

The figures in Tables I and II, which are selected from results recorded by Kiesselbach (5), show that absence of manure, or reduction in size of pot, both of which curtail the supply of nutrient salts, cause not only a reduction in the dry-weight of the plant but also a reduction in the leaf-area. The latter reduction, however, is smaller than that of the dry-weight, and consequently the average rate of increase in dry-weight per unit leaf-area, which is a fair

Table I.—Effect of Size of Pot on Yield—Maize, Kiesselbach.

Size of pot.	Soil in pounds.	Dry-weight of plant in grm.	Leaf-area in sq. cm.
12″ × 12″	32·5	269	1167
12″ × 24″	85	402	1353
21″ × 36″	583	708	1405
30″ × 36″	956	781	1287

Table II.—Increase in Yield by Manure—Maize, Kiesselbach.

Size of pot.	Increase dry-weight over unmanured.	Increase leaf-area over unmanured.
12″ × 12″	276 per cent.	166 per cent.
30″ × 36″	107 „	101 „

comparative measure of the average rate of assimilation per unit leaf-area, is considerably reduced by reducing the supply of nutrient salts.

A deficiency of nutrient salts may reduce the average rate of assimilation per unit leaf-area in many ways. It may be that the growing parts of the plant cannot utilise the carbohydrates as rapidly as the leaves can synthesize them; under such conditions, the leaves would become packed with carbohydrates which might reduce the assimilation, either by causing a closure of the stomata, or by direct effect on the photosynthetic mechanism. Or, it may be, that the deficiency of nutrient salts acts directly on the photosynthetic mechanism. In the latter case, the average rate of assimilation is reduced by decreasing the actual rate throughout the whole period. In view of the close correlation between the results of growth experiments and experiments on photosynthetic activity recorded previously (1 and 2), it was decided to investigate the effect of deficiency of nutrient salts on photosynthetic activity, a subject which, apart from chlorosis caused by lack of iron, does not seem to have received attention as yet.

To determine this a plant was chosen with a good initial store of food, so that, when grown on nutrient solution devoid of a particular element, the effects of a slight shortage of this element could be investigated. *Phaseolus vulgaris,* a plant of which the assimilation had been investigated from several other points of view, was found suitable for this work. The seeds (Sutton's "Monster Negro") were chosen as uniform as possible, and were germinated on moist sphagnum or silica sand. The culture solutions were made up from Sachs' mixture and tap water.*

In the first series of experiments, the results of which are presented in Table III, the assimilation of the primary entire leaves of the plant was tested just before the next (the first pinnate)† appeared. Two different light intensities were used, the approximate values being 9,000 lux and 36,000 lux respectively. The exact value is of no great importance, the main point being

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* The solution devoid of potassium was made by replacing KNO_3 by an equivalent amount of $NaNO_3$, that devoid of phosphorus by replacing calcium phosphate by nitrate, that devoid of magnesium by replacing $MgSO_4$ by $CaSO_4$, that devoid of iron by omitting the addition of a small piece of rusting iron.

† The assimilation was measured by the method described in a previous paper (1), the oxygen being removed by palladium black in the presence of hydrogen.

Table III.—First Series of Experiments.

Date.	Culture solution.	Leaf.				Intensity of illumination.	Temperature.	Assimilation in c.c. O_2 per hour per 50 sq. cm. leaf.		
		Area.	Fresh-weight.	Dry-weight.	Area/Dry-weight.			Apparent assimilation (observed).	Real assimilation (calculated).	
									Light-limited (9000 lux).	Temp.-limited (15° C.).
		sq. cm.	mgrm.	mgrm.		lux.	° C.			
19.3.20	Sachs normal	7·2	221	22	0·325	9,000	14·1	2·36	2·57	5·71
						36,000	14·9	5·42	—	
19.3.20	Without Mg	7·3	215	20	0·365	9,000	14·2	1·90	2·11	4·70
						36,000	15·2	4·66	—	
20.3.20	Without P	4·5	141	14·5	0·310	9,000	14·8	2·41	2·64	5·54
						36,000	15·8	5·60	—	
21.3.20	Without Fe	4·6	126	14	0·330	9,000	14·5	2·14	2·34	4·67
						36,000	15·1	4·45	—	
21.3.20	Without K	5·25	152	20	0·265	9,000	15·2	2·00	2·22	5·47
						36,000	15·0	5·19	—	

Assimilatory activity of first developing leaves of young plants of *Phaseolus vulgaris* grown on various culture solutions. Seeds sown in silica sand 9.2.20; transferred to the culture solutions 19.2.20; grown in south window of laboratory.

that with the lower intensity the external limiting factor was light, while with the higher it was temperature which was limiting the rate of assimilation.* It is obviously of theoretical importance to determine how these two states, reflecting the photochemical and the chemical phases of the process, are influenced by this treatment.

In all the experiments in this paper, photosynthetic activity is directly measured as oxygen produced, and is stated as cubic centimetres O_2 per hour per 50 square centimetres leaf area. These values are, of course, those of "apparent assimilation." The values of respiration used in converting these to "real assimilation" are based on a value, well established for normal leaves of *Phaseolus*, namely, 1·5 c.c. per gramme dry-weight per hour at 15° C. For calculation from this standard to the temperatures of the individual experiments, which range from 11° C. to 19° C., a temperature coefficient of 2·0 for a rise of 10° C. was employed.

The last two columns of the Tables contain respectively the calculated values of real assimilation for a limiting light of 9000 lux, and a limiting temperature of 15° C., arrived at as follows:—For the former, the observed apparent assimilation (column 9) had to be increased by the addition of the respiration appropriate to 50 sq. cm. of that particular leaf at the temperature of that particular experiment (column 8). The respiration number for 15° C. is, in each case, $= 1{\cdot}5 \text{ c.c.} \times [\text{dry weight (column 5)}/\text{leaf area (column 3)}] \times 50$; from this the value at the temperature (column 8) is obtained by the temperature coefficient of 2·0.

For the temperature-limited values of the last column, the observed apparent assimilation must be converted from the temperature of column 8 to 15° C., using again a temperature coefficient of 2·0 for the assimilation also. To this is then added the respiration at 15° C. appropriate to a leaf of that particular area/dry-weight ratio as shown above.

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* That temperature and not light actually was the limiting factor with the higher intensity of illumination (36,000 lux) is shown by the following considerations:—With the temperature under 20° C. (in none of the experiments did the temperature exceed this limit) no higher value of assimilation was obtained by increasing the intensity of illumination from 36,000 to 55,000 lux, either with normal leaves or with those from plants grown on culture solution devoid of some element. Further, with the intensity of illumination of 36,000 lux and a temperature 25° C., values nearly twice as big as those estimated for 15° C. were obtained. These values for 25° C. are in agreement with those recorded by Willstätter and Stoll (12) for *Phaseolus* at that temperature. Admittedly their experiments were carried out with an illumination of 48,000 lux, as compared with 36,000 lux in the present experiments, yet a doubling of assimilation cannot be attributed to an increase in illumination of 33 per cent. In all the experiments carbon dioxide was maintained in excess throughout. Evidence that this was done is provided by the fact that, although the experiments were conducted in a closed atmosphere, so that continuance of assimilation steadily reduced the concentration of the CO_2, yet the values of assimilation, successively determined, did not decrease, as they would were CO_2 limiting, but kept on at a constant value so long as there was no alteration of light or temperature.

Setting out all the results in this comparable form, it is easy to compare the relative effect of each nutrient salt deficiency on the light-limited values with the effect of the same treatment on the temperature-limited values.

Although in external appearance the leaves from the different plants were indistinguishable, and such was the case in all the series of experiments with the one exception mentioned below, yet it will be seen from the Table that in the case of the plants grown in the solutions devoid of magnesium and iron respectively the photosynthetic power of the leaves was decidedly lower, whether light or temperature was limiting, than that of those in normal solution. From the small size attained by these leaves compared with those of plants grown later in the year there is good reason to believe that the food reserves of the cotyledons were not exhausted at this stage. Hence the evidence is that a *slight* shortage of magnesium or iron resulted in a reduction of the photosynthetic activity, both when the external limiting factor was light and when it was temperature. The smaller values with the higher light intensities are not due to the leaves of the plants grown without magnesium or iron being thinner, since the values are smaller when expressed per unit weight as well as when expressed per unit area. Müller (9) suggests that the reason why shade leaves assimilate less per unit area than do sun leaves whilst the values for assimilation are the same when expressed per unit weight is because the former are thinner.

After the removal of one leaf from each, the plants were left without change of culture solution until the second pair of leaves had begun to develop. At this stage the assimilatory power of these pinnate leaves was measured under conditions similar to those of the first experiments. The results of this second series, which are recorded in Table IV, confirm the conclusions drawn from those of the first. It will be seen also that a shortage of phosphorus has at this stage made itself evident by a reduction in the assimilatory power of the leaves. It was not so marked in the first leaves.

Another feature of interest is that the assimilatory power of the plant grown in normal water culture solution was lower than that of the plant grown in soil in a pot (*cf.* Table VI). As the plants were grown in the laboratory for some considerable time, it was thought that the harmful effects of the laboratory air might possibly have been responsible for this difference, but as the results of the next experiments with plants grown under the same atmospheric conditions as pot plants showed the same difference, the explanation must be sought in other directions.

Table IV.—Second Series of Experiments.

Date.	Culture solution.	Leaf.				Intensity of illumination.	Temperature.	Assimilation in c.c. O_2 per hour per 50 sq. cm. leaf.		
		Area.	Fresh-weight.	Dry-weight.	Area/Dry-weight.			Apparent assimilation (observed).	Real assimilation (calculated).	
									Light-limited (9000 lux).	Temp.-limited (15° C.).
		sq. cm.	mgrm.	mgrm.		lux.	° C.			
19.4.20	Without Mg	6 ·65	150	22	0 ·30	9,000	11 ·8	1 ·93	2 ·12	3 ·20
						36,000	11 ·4	2 ·30	—	
20.4.20	Normal	18 ·25	342	51	0 ·36	9,000	11 ·3	2 ·39	2 ·56	3 ·95
						36,000	11 ·9	3 ·02	—	
21.4.20	Without Fe	4 ·2	83	11 ·5	0 ·36	9,000	11 ·2	1 ·53	1 ·69	2 ·77
						36,000	11 ·8	2 ·06	—	
22.4.20	Without P	10 ·1	192	26 ·5	0 ·38	9,000	13 ·2	2 ·01	2 ·17	3 ·26
						36,000	12 ·5	2 ·58	—	
22.4.20	Without K	7 ·9	166	30	0 ·26	9,000	13 ·4	2 ·36	2 ·61	3 ·95
						36,000	13 ·0	3 ·19	—	

Assimilatory activity of the first pinnate leaves, developing after the first entire leaves, of the plants of *Phaseolus* used in the first series of experiments. Sowing dates given in Table III.

Table V.—Third Series of Experiments.

Assimilatory activity of leaflet of first pinnate leaf of *Phaseolus* plants grown on various culture solutions in the open air. Seeds sown in sphagnum 26.4.20; transferred to culture solutions 8.5.20.

Date.	Culture solution.	Leaf.			Intensity of illumination.	Temperature.	Assimilation c.c. O_2 per hour per 50 sq. cm. leaf.			
		Area.	Dry-weight.	Area/Dry weight.			Apparent assimilation (observed).	Real assimilation (calculated).		
								Light-limited.		Temp.-limited (15° C.).
								1,250 lux.	9,000 lux.	
		sq. cm.	mgrm.		lux.	° C.				
28.5.20	Normal	13·2	43·5	0·30	1,250	19·0	0·38	0·69		
					9,000	18·2	2·50	—	2·79	
					36,000	17·7	3·75	—	—	3·35
29.5.20	Without Mg	19·6	55·8	0·35	1,250	16·4	0·21	0·45		
					9,000	17·4	1·27	—	1·53	
					36,000	18·0	2·40	—	—	2·16
30.5.20	Without Fe	9·6	25·9	0·37	1,250					
					9,000	16·0	0·34	—	0·56	
					36,000	16·5	0·71	—	—	0·84
31.5.20	Without K	18·6	57·0	0·33	1,250	15·2	0·32	0·55		
					9,000	15·5	1·64	—	1·88	
					36,000	15·6	2·66	—	—	2·78

Table VI.

(Headings as above.)

		sq. cm.	mgrm.		lux.	° C.				
3.6.20	Pot-grown	12·6	48	0·26	1,250	15·6	0·42	0·72		
					9,000	17·2	2·98	—	3·31	
					36,000	17·6	5·65	—	—	5·00

Assimilatory activity of first pinnate leaf of *Phaseolus* grown in pot in open air.

For the third series of experiments water cultures were set up on the roof of the Cambridge Botany School; the plants developed much larger first leaves than plants grown in pots and looked altogether quite as healthy. When the pinnate leaves appeared, however, unlike the similar plant in the first set of cultures, the plant which was not supplied with iron produced a chlorotic leaf. The explanation of this may be that in the second set of cultures the store of iron in the cotyledons had been exhausted by the first leaves. The plant grown on the culture solution devoid of iron behaved differently from that grown without nitrogen in that whilst in the latter case the first leaves died off as the second leaves appeared, the small amount of nitrogen present presumably having been transferred to the new leaves; in the former the first leaves remained green, the chlorosis spreading into the second leaves upwards from the petiole.

The results of this set of experiments recorded in Table V bear out the general conclusions drawn from the previous ones. In each of the three cases where one element of the normal solution was missing the assimilatory power of the leaves was markedly less than that of the leaves of the plant grown on the normal solution. This time the assimilation was measured at a still lower light intensity than in the previous cases. Under such conditions the normal plant still shows greater activity than the others.

Theoretical Considerations.

In this section it is proposed to analyse the results from the point of view that the photosynthetic process consists of photochemical and chemical phases. The diffusion phase can in this case be left out of consideration, since in all experiments carbon dioxide was present in such quantities as to ensure that this stage did not limit the rate of reaction as a whole. As was stated above, two intensities of illumination were used; with the lower, light was the external limiting factor—in other words, the rate of the photochemical phase limited that of photosynthesis; with the higher, temperature was limiting, that is, the rate of the chemical phase determined the rate of photosynthesis. It is fully realised that in a complex structure such as that of a leaf, under certain conditions of illumination one part of the leaf may receive sufficient light energy, so that the rate of photosynthesis may be temperature-limited, whilst another part less favourably situated, the back for example, may have its rate of photosynthesis light-limited; but the intensities of illumination were such that practically the whole of the leaf was so illuminated that the rate of photosynthesis was limited either by light or by temperature, according to the intensity of illumination used.

For the purpose of comparison, the results of the different series have been brought together in Table VII, where they are also expressed as percentages. For the second and third series of experiments, with first pinnate leaves, the values are related to the corresponding leaves of the plant grown in a pot taken as 100. For the first series, with the first simple leaves, the standard is the plant grown in the normal culture solution, since this was practically the same as that of the plant grown in a pot.

It may be pointed out that the relations established do not much depend on the adopted temperature coefficients of 2·0 being accurate. The coefficients would have to be widely different indeed if the conclusions were to be in any way modified by them.

From an inspection of the above Table it will be seen that the subnormality of the photosynthetic activity of the plants grown on culture solutions lacking certain elements, becomes more marked in passing from the first series to the third. This, no doubt, is to be attributed to the fact that, since the growth made was progressively greater in the later experiments, and since the food supply of the cotyledons had already been exhausted, the deficiency of mineral nutrient was progressively greater. Further, the plants grown on normal solution show subnormal activity as compared with pot-grown plants. This suggests that here also the plants may have been experiencing a shortage of mineral nutrient. This point is worthy of consideration when dealing with water-cultures generally.

Subnormal Assimilation.

Previously the author has shown that in seedlings which do not develop their photosynthetic activity until after germination the activity is subnormal both when light and when temperature is limiting (1–2). The figures in the above Table show that in this case also the activity is subnormal whichever of the factors is limiting, in other words that subnormality in the photochemical phase is accompanied by subnormality in the chemical phase. But the most striking fact of all is that in practically all cases *both phases show the same degree of subnormality.*

Before considering the bearing of the above facts on our conception of the photosynthetic process it will be well to consider other cases of subnormal assimilation, and see whether the dual effect on photochemical and chemical phases is general.

In the leaves of cherry-laurel there is a well-marked *seasonal* change in the photosynthetic activity. The leaves show a fall in activity about March or April, the exact time depending upon the weather conditions prevailing. A consideration of the data in Miss Matthaei's paper (7) shows that the seasonal change affects both the photochemical and the chemical phases. A comparison of figs. 1 and 2 in the above paper shows that the assimilation falls

Table VII.—Summary of Results.

Leaves.	Factor, limiting.	Real assimilation per 50 sq. cm.											
		Pot plant.		Various water cultures.									
				Normal.		Minus Mg.		Minus P.		Minus Fe.		Minus K.	
		Absolute.	Per cent.	Absolute.	Per cent.	Absolute.	Per cent.	Absolute.	Per cent.	Absolute.	Per cent.	Absolute.	Per cent.
First simple leaves, Table III	Light	—	—	2·57	100	2·11	82	2·64	103	2·34	91	2·22	87
	Temp.	—	—	5·71	100	4·70	82	5·54	97	4·67	82	5·47	96
First pinnate leaves, Tables IV, V and VI	Light	3·31	100	2·56	77	2·12	64	2·17	65	1·69	51	2·61	79
	Temp.	5·00	100	3·95	79	3·20	64	3·26	65	2·77	55	3·95	79
	Light	—	—	2·79	84	1·53	46	—	—	0·56	17	1·88	57
	Temp.	—	—	3·95	67	2·16	43	—	—	0·84	17	2·78	56

The results with pinnate leaves are expressed as percentages of the assimilation of the same leaves on a plant grown in a pot; those for the first simple leaves are related to the normal water culture as 100, since the leaves of the latter are practically the same as the first simple leaves of a plant grown in a pot.

Table VIII.—Photosynthetic Activity of Leaves at varying Stages of Development—*Helianthus annuus*.

Date.	Area.	Dry-weight.	Light intensity.	Temperature.	Assimilation. O_2 per 50 cm.^{2} per hour at 15° C.	Remarks.
	cm.^{2}.	mgrm.	lux.	° C.	c.c.	
8.8.20	15·1	94	9,000	16·7	1·73	Young leaf from a plant nearly fully-grown.
			36,000	16·7	2·29	
7.8.20	9·8	52	9,000	15·4	2·53	Young leaf from plant half-grown.
			36,000	15·7	3·08	
16.6.20	16·7	78	9,000	18·8	4·52	Half-grown first foliage leaf.
			36,000	19·1	7·53	

from 2·8 mgrm. of CO_2 per 50 square centimetres to about 2·1 mgrm. when the light intensity (one in Miss Matthaei's units) is limiting, whilst a comparison of figs. 4 and 5 reveals a fall from 12·7 to 10·1 mgrm. when the assimilation is limited by a temperature of 25° C. Again it will be noticed that the percentage fall is about the same in both cases, 25 per cent. in the former and 20·5 in the latter.

Willstätter (12) has shown that the young developing leaves of certain trees show a subnormal activity when temperature is limiting, but he records no results when light is limiting. Table VIII, which contains results of experiments carried out by the present writer, shows however that in the developing leaves of medium-aged and older plants of *Helianthus annuus* the activity of both phases is subnormal when compared with a fully developed leaf. Further, Willstätter's experiments show that the same holds when leaves of the yellow varieties (here the subnormal) are compared with leaves of green varieties of the same species (see p. 149). In the last two cases, however, the subnormality is not of the same degree in both phases; in *Helianthus* the chemical phase shows the greater depression, whilst in the yellow leaves it is the photochemical. Thus depression of both phases to a more or less equal extent seems to be of fairly general occurrence in cases of what may be called subnormal assimilation.

That the condition of affairs as stated above is not necessarily what might be expected is shown by Miss Matthaei's remark, in the paper referred to above, that "it appears as if in the sluggish condition of the leaves more light was necessary to do the same amount of work." This clearly is the case when light is limiting the rate in the subnormal leaves, and there seems no *a priori* reason why, when temperature is limiting, a sufficient increase in the intensity of the illumination should not enable the subnormal leaves to attain the same value as the normal, in other words that subnormality is all a question of intensity of illumination. That such is not the case, however, is clearly shown for the subnormal leaves of *Phaseolus* seedlings (2) and by Willstätter for leaves of yellow varieties, and indeed is fundamental to Matthaei's argument that in both the latter cases quoted the temperature of 25° C. was limiting.

A simple explanation of these striking facts is arrived at if we picture the photosynthetic mechanism as a heterogeneous reaction, with its activity necessarily determined by its active surface, in the following way. From the point of view of chemical dynamics the most fruitful way of expressing the rate of a reaction is in terms of the concentration of the reactants, whatever the modifications necessary to explain the effect of temperature on the rate may be. In the process of photosynthesis the reactants are carbon dioxide, light and some constituent of the leaf, this latter including beside chlorophyll something of a protoplasmic nature. Whatever part the pigments may play, photocatalytic or otherwise, the rate of photosynthesis will be a function of the amount of reactive substance within the leaf. Not knowing how to measure all the latter, assimilation rates have been expressed in terms of leaf-area, dry-weight or fresh-weight. More recently Willstätter has expressed his results per unit of chlorophyll-content (assimilation-number). It might have been expected that when light was the external limiting factor the assimilation would bear some relation to the amount of chlorophyll, but although that author has much discussion as to whether an increase in assimilation under various conditions is due to an increase in chlorophyll or to what he calls the enzymatic factor, yet in practically all his experiments the limiting factor is not light but temperature. His experiments with yellow and green leaves, however, show that if there be any direct relation between the rate of assimilation and the chlorophyll-content it is far from being a linear one whether light or temperature be limiting.

The conception of the process of photosynthesis which seems best to fit the facts is that the seat of the process is the *surface* of the chloroplast, for here the proportion of light absorbed will tend to be greater, and this will be the portion of the chloroplast with which the carbon dioxide will first come into contact. To give more detail to the picture, we may postulate that the photochemical phase of the process consists of an activation, by means of light energy, of the molecules of the surface of the chloroplast either before or after combination with carbon dioxide, and that the chemical phase is an interaction of such activated molecules (including the carbon dioxide). The speed of the latter is considered as being slow compared with removal of the products.* The rate of the first phase will not be affected by temperature, whilst that of the latter will.

When carbon dioxide is in excess, that is, when more molecules of that substance strike the surface in unit time than can be activated or enter into combination with the activated molecules of the surface, and when the temperature is such that the activated molecules interact and are removed as quickly as they can be formed, then the rate of the process as a whole is limited by light. Similarly, when the carbon dioxide is in excess, and when the amount of light energy of the requisite wave-length falling on a given surface is greater than that required to activate the number of molecules which can interact in unit time on that surface, then temperature is limiting. Carbon dioxide is limiting when the light and the temperature are such that more molecules than those striking the surface in unit time can be dealt with. It becomes clear that the fundamental quantitative factor in this mechanism is what may be termed the *amount of reactive chloroplast surface.* Any variation in this internal factor will affect the photosynthesis in direct proportion whether the external conditions are so arranged that light or that temperature is limiting.

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* See Langmuir's views on heterogeneous reaction velocity (6).

That this reactive surface is not always necessarily identical with the actual visible surface of the plastid is shown by the fact that the yellow and green leaves examined by Willstätter (12, p. 110), although exhibiting different photosynthetic activity, had the same size and number of chloroplasts, and hence the same chloroplast surface.' Further evidence in this direction is afforded by the fact that, in the developing seedling leaves of *Phaseolus,* no appreciable change in size or number of chloroplasts could be detected, whilst the photosynthetic activity increased considerably. It is possible that, in the case of the yellow leaves, there was not sufficient chlorophyll to render the whole chloroplast surface active, whilst in the seedling leaves some change in the state of the chlorophyll may have been taking place, thus resulting in the increase of the amount of "reactive surface"; the amount of chlorophyll was constant.

Other things being the same, however, a change in the size of the chloroplast would result in a change in the amount of "reactive surface." It is interesting to note in this connection that Meyer (8) records the following changes in the size of the chloroplasts of *Tropœolum majus* as the leaves become older and their colour changes from dark green to yellow. If the diameter of the chloroplasts in a dark green leaf be taken as unity, the diameter in the case of a green, a pale green, and a yellow leaf respectively was found to be 0·86, 0·72 and 0·52. The corresponding surface would be 1·00, 0·74, 0·52 and 0·27. Since there is no tendency for increase in number of chloroplasts to accompany this ageing process, the decrease in "reactive surface" should be at least of this order. Gris (3) records similar decreases in the size of chloroplasts for plants suffering from iron chlorosis and for plants deprived of light. Moreover, the same author found that the chloroplasts of the young leaves of *Phaseolus* and other plants increase considerably as the leaves develop.

It follows, therefore, that any change in the amount of "reactive surface" per unit of leaf (area or weight) will necessitate a change in the photosynthetic activity, both when light and when temperature is limiting. Doubling the amount of "reactive surface" should double the activity when temperature is limiting, just as in simple cases of enzyme action doubling the concentration of invertase doubles the rate of inversion of sucrose (9); also, under ideal conditions, *i.e.*, where the whole surface of the chloroplast is equally illuminated, it should double the amount of light absorbed, thus doubling the activity when light is limiting. Such a proportional change in activity seems to hold for the case of *Phaseolus* recorded in this paper, and for the case of seasonal change in Cherry Laurel. But in a complicated structure like that of a leaf, with its many internal reflecting surfaces, it would be surprising if the ideal conditions held, for a change in the amount of reactive surface might be accompanied by a change in the structure of the leaf.

As an extension of this conception one must anticipate further that when carbon dioxide is limiting, as in natural vegetation, subnormality will find expression in the same way. The coincidence of subnormal photosynthetic activity and subnormal rate of growth in various seedlings in the ordinary atmospheric supply of carbon dioxide (1 and 2) is remarkable, and similar coincidence for plants with insufficient mineral nutrient has been demonstrated above. Although, as was stated at the beginning of this paper, subnormal growth does not necessarily signify subnormal photosynthetic activity when carbon dioxide is limiting, yet in the absence of evidence to the contrary it is suggestive that such is the case. Irving's experiments (4), however, definitely show that certain seedlings show subnormal activity when carbon dioxide is limiting, and some of the seedlings were the same as those used by the present writer (1). Plester (11) found that yellow-leaved plants, growing in the open, exhibit an activity subnormal as compared with that of green varieties of the same species. Since in the cases investigated the stomata of the yellow varieties were both more numerous and larger than those of the green the difference cannot be attributed to this cause. Admittedly, as Willstätter justly points out, Plester used the "half-leaf method" without realising its shortcomings. Nevertheless, despite this and the fact that the two workers used different material (with the exception of *Ulmus montana* and *Acer pseudoplatanus*), the results as a whole strongly suggest that subnormality expresses itself no matter whether carbon dioxide or some other external factor be limiting.

Apart from the above conception of the photosynthetic process, or some such similar one, there seems no reason why a leaf of yellow elm, which in a laboratory experiment with CO_2 in excess, at a temperature of 25° C. and an intensity of illumination of 48,000 lux, conditions not better than those holding on a summer day, can absorb carbon dioxide at the rate of 2·93 grm. per square metre per hour (12), should, on a bright summer day under open air conditions of carbon dioxide supply, absorb carbon dioxide at the rate of only 0·3 grm. per square metre per hour, whilst a leaf of green elm absorbs as much as 0·8 grm. under the same conditions. In other words the photosynthetic mechanism of the yellow leaf, *apart from its smaller reactive surface*, would appear to be capable of dealing with at least as much carbon dioxide as that absorbed by the green leaf. Though there is as yet no way of checking this hypothesis by evaluating the "reactive surface of the chloroplast," this treatment of the dynamics of photosynthesis at least finds some justification in the way that it unifies and interprets all the phenomena of subnormality.

Summary.

The photosynthetic activity of plants of *Phaseolus vulgaris* grown on culture solutions devoid of potassium, magnesium, iron or phosphorus is less than that of plants grown on full culture solution. When the second leaves appear the activity of the latter also is less than that of plants grown in soil.

The activity is shown to be depressed in each case to the same extent when light is limiting as when temperature is limiting.

Other cases of such a coincidence are quoted from literature; namely, seasonal change in cherry laurel, yellow varieties as compared with green, developing seedling leaves of certain plants and developing leaves on more or less mature plants of *Helianthus annuus.*

Moreover, not only is the photosynthetic activity subnormal when light and when temperature are limiting, but evidence is produced that such is the case when carbon dioxide is limiting.

A conception of the nature of the photosynthetic process is put forward to explain the above facts. The chief point in the conception is that the factor inside the leaf which is involved in the process is the amount of "reactive chloroplast surface." This is not necessarily the same as the actual chloroplast surface. Increase in the amount of "reactive surface" will involve a corresponding increase in the photosynthetic activity when a given temperature is limiting, and under ideal conditions a corresponding increase when a given intensity of illumination or partial pressure of carbon dioxide is limiting. It is pointed out that the conditions in the leaf are not always necessarily ideal.

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The Progress of Metabolism after Food in Swine.

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The results described in the present paper have emerged in the early stages of what is intended to be a comprehensive investigation of the course of metabolism in swine when age, weight, food, temperature of surroundings, etc., vary.

Measurements have been made of the heat evolution of a fasting hog at various stages of fasting up to a maximum of six days, and at various temperatures ranging from 10° C. to 20° C., by means of the calorimeter described by one of the writers (J. W. C.) in the 'Journal of Agricultural Science' for October, 1921.

The hog used has been the same throughout—a pedigree large white, bred by Mr. K. J. J. MacKenzie at the University Farm. The animal was a male which had been castrated at the age of 9 weeks. When the observations began on November 28th, 1921, his age was 10 months and he weighed